

INFORMATION ABOUT BEHAVIOR IS PROVIDED BY SONGS OF THE STRIPED CUCKOO

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ABSTRACT.—Striped Cuckoos (*Tapera naevia*) have three different song types. We investigated behavioral correlates of two using interactive playback to simulate territorial intrusion. Individuals sang one song type frequently when not interacting closely with neighbors, mates, or playback. A less common song type was sung by subjects that had approached playback closely, and by closely countersinging neighbors. These two song types distinguish different extents to which a singer may take initiative leading to interaction: the first provides information that the singer will probably stay put and not interact closely unless approached, the second that the singer will itself approach and search for another individual. Such distinctions are significant because they parallel recent results from diverse passerines, and because the information may be fundamental in enabling singers to obviate or elicit encounters with distant individuals. Received 6 July 1998, accepted 10 June 2000.

Diverse animals at times signal in sequentially ordered, near-rhythmic bouts termed singing (Smith 1991), the structural properties of which transcend major phylogenetic boundaries. What singing offers may be information that is especially important to individuals when out of each other's sight.

Information refers here to any property of objects or events that facilitates predictions about them (Smith 1997). Information thus reduces uncertainty. Even markedly different kinds of animals have common informational needs. For instance, animals often must monitor each other's locations and activities. Songs (the main components of singing performances) help by providing some information about identity (Becker 1982, Falls 1982, Nelson 1988) and location (Wiley and Richards 1982, Naguib 1995). Additional information contained within a song includes aspects of a singer's behavior and can influence the likelihood of close interactions. Despite its significance, such information has received little attention (see partial reviews by Dabelsteen 1985; Smith 1977a, 1991; Spector 1992).

When a bird matches a song type uttered by a neighbor, it provides information concerning both its attentiveness to that neighbor and its readiness to interact. However, individuals of many species do not match songs. Instead, they select among different song types and variants, making available infor-

mation about the extent to which they will take initiative in interacting. Most simply, a singer indicates the probability that it will either actively seek out and approach other individuals or remain where it is, responsive but leaving further initiative to others. Such information should help mates, neighbors, or strangers decide whether to interact closely with a singer, negotiate (see Discussion), or remain apart and accept the singer's current behavior.

We make no inferences about the extent to which songs' information enables reliable prediction (is "honest"). Our interpretations are empirical, based on what we see singers do when uttering different songs. Once known, the same types of behavior that correlate with a vocalization when the singer is visible can be expected to occur even when the signaler is unseen. The same information is also available to listening birds. If signaling is deceitful, the correlations break down.

We used playbacks and observations of behavioral responses to ask whether the widely shared structural and functional properties of singing provide types of information that are fundamentally similar among oscine, suboscine, and nonpasserine birds. Our goal—unusual for playback experiments—was not to compare effects of different stimuli but to affect subjects' behaviors. We asked what they sang in conjunction with specific behaviors. A song type correlated with a specific behavior could inform listeners that a singer is engaged in that behavior. We used playbacks to elicit behavior that is difficult to observe in actual disputes. We compared behavioral informa-

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TABLE 1. Playback stimuli and the kinds of vocalizations uttered by each subject before playback and in its initial singing when close to playback.

Subject	Playback stimulus		Preplayback singing			Initial vocalizations when close	
	<i>Sem-fim</i>	<i>Wee</i>	<i>Sem-fim</i>	<i>Wee</i>	Silent	Brief tones	<i>Wee</i>
1	1		X			X	X
2	1		X			X	X
3	1		X			X	X
4	2		X			X	X
5	2		X			X	X
6	2		X			X	X
7	3		X			X	X
8	3		X			X	X
9	4		X			X	X
10	4			X ^a		X	X
11	4		X			X	X
12	5			X ^b		X	X
13	6				X	? ^c	X
8		1	X			X	X
14		2	X			X	X

^a Bird #10 was not countersinging before playback, but was apparently with a mate that uttered a *feeee*-series song.

^b Bird #12 was countersinging with a neighbor before playback began.

^c Bird #13: recording failed during the first part of this trial. We may have failed to hear faint brief tones in the field.

tion provided by songs of the nonpasserine Striped Cuckoo (*Tapera naevia*) with that made available by songs of passerines studied previously (Smith 1988; Smith and Smith 1992, 1996a, b).

The cuckoo is a resident of scrubby pastures, llanos, and cerrados from Mexico to Argentina. Individuals often sing from bush-tops and even trees, but are otherwise inconspicuous. They forage amid vegetation, primarily on or near the ground and readily run (Howell and Webb 1995). Each of their three song types has a distinctive behavioral correlate.

METHODS

Field work was done from 1–9 July 1989 and 28 May–13 June 1992 on Hato Piñero, a ranch and nature preserve of 26,000 ha in the llanos of Cojedes, Venezuela. Each of the 14 unmarked experimental subjects was on a separate site. We made additional notes on another eight individuals that were not involved in experiments.

Our observations and an account by Sick (1953) led us to predict that at least two of the three different song types (termed *sem-fim* and *wee*-series) would be uttered in conjunction with distinctive interactional behaviors. Our tests involved simulating spatial intrusions to elicit approach and search. Search was operationally defined as conspicuous scanning movements, often involving perch changes. We compared vocalizations uttered in conjunction with approach and search behavior to pre-playback samples of 5–50 songs and post-playback samples of 2–5 min/bird.

Our playback was interactive. We adjusted it within preset limits to the behavior of each subject as a trial developed because each subject had its own experiences and temperament and responded uniquely. Presumably, subjects did not expect to encounter an intruder that did not interact but repeated songs on an irrelevant schedule. Our interactive trials therefore differed from one another in details that inevitably differ in natural encounters.

Our procedures were one of two types of interactive playback. One uses a fixed speaker position and predetermined rules to alter the stimuli that are played back (Dabelsteen and Pedersen 1990, Dabelsteen and McGregor 1992). Instead, we interacted by adjusting the timing of playback of a single type of stimulus relative to each subject's actions. This allowed us to accommodate to the subject's rate of approach and vocalization and to move the playback speaker to simulate an elusive intruder's probing, evasive movements (Smith 1988, 1997; Smith and Smith 1992, 1996a, b).

Each subject was located by its loud singing. We began recording when we had approached to 50–100 m from the bird, and continued until the subject approached to within 20 m. For four subjects that did not approach promptly we interrupted playback and moved to a nearby location one to three times (not more than once per min). One of us kept the speaker facing the subject and in vegetation that could conceal an intruder to provide the subjects a site to search. Each subject was used once, except subject 8 (Table 1); it first heard *sem-fim* playback and then *wee*-series playback. No subject heard the playback of a neighbor's song.

Continuous playback of *sem-fim* to nine subjects contained 5 s natural silent intervals between songs.

Four other subjects sang rapidly and continuously, and we played back single *sem-fim* songs in answer to every second, third, or fourth of their songs. We stopped playing a song when a subject closely approached the speaker. However, for six subjects that became silent after approach, we eventually played single songs or brief bouts of *sem-fim* faintly from one to three nearby sites. *Wee*-series songs were played back to only two subjects. Recording continued until all but one subject had reverted to *sem-fim* singing or become silent.

We used a Sony TC-D5M stereo cassette recorder and an electret microphone (Radio Shack 33-1060) on a Sony PBR-330 parabola. Behavioral notes were dictated onto the parallel recording track. Playback was from a Sony CFS-W50 recorder with a 1 watt speaker, adjusted to sound as loud as a cuckoo singing 35 m away (corresponding to an SPL of 75–82 db, 1 m from the speaker). Playback to the six subjects that initially kept silent after approaching was at 58–62 db, simulating the faintness with which other subjects first responded when close.

Playback stimuli were previously recorded songs, each from a different individual. We lacked sufficient subjects and time to complete controls with *wee*-series stimuli, partly because four *sem-fim* stimuli were each played to more than one subject (Table 1) to obtain at least one well recorded trial with each stimulus. (We could not, in the field, adequately assess faint vocalizations.)

Vocalizations were analyzed on a Kay Elemetrics DSP-5500 sound station, using a transform size of 100 points (150 Hz) on a 0–4 kHz frequency range and the Hamming windowing function. Significance was evaluated by the two-tailed sign test (Siegel 1956).

RESULTS

Fourteen subjects approached the playback speaker and sang. Most came within 10–20 m and progressed consistently through two song types and several different faint tones while performing several visible displays. A third song type was recorded but not during approaches.

Vocalizations.—The most common song was a clear, rising couplet (Fig. 1A). The Brazilian name for the bird, *sem-fim*, means “without end”, apt for a song that is sometimes repeated all day and all night (Sick 1953). Slight variation in frequency and duration was common, but abrupt frequency shifts, broken components, and greatly shortened inter-component intervals were rare. Nearly all *sem-fim* songs were monotonously alike.

A less common song had an ascending series of usually 4–7 (range: 1–16) *wee* components, with each component increasing

slightly in frequency and amplitude. Inter-component intervals were briefer than in most *sem-fim* songs. Most of an individual’s simple *wee*-series songs began lower than its *sem-fim* but finished at least as high (Fig. 1B). “Elaborated” *wee*-series songs terminated with a flat or descending component of lower frequency (Fig. 1C).

The rarest song type was a series of gently rising, 0.3–0.5 s components, arbitrarily termed *feeee* (the audible distinction between *feeee* and *wee* is not fit by our alphabet). Figure 1D shows a *feeee* song of three components being answered by another individual’s couplet of elaborated *wee*-series songs. Most of the 37 recorded *feeee*-series songs had two to four components. Simple and elaborated forms occurred, as in *wee*-series songs.

Hardest to characterize were extremely faint, brief tones (Fig. 2). We heard these only when within 10–15 m of a subject. The parabola mounted microphone detected many cases we did not hear in the field, but may have missed others. Consequently, we made no statistical analyses of their occurrence.

Such tones were variable and many resembled abbreviated components of songs, condensed songs, or fragmented songs (Fig. 2A, B); most resembled *wee* more than *sem-fim*. One subject divided components of *wee*-series songs into brief segments (Fig. 2C), each indistinguishable from the briefest tones of other individuals. Overall, brief tones comprised few of the recorded vocalizations and had narrowly defined uses (see below).

Visible display behavior.—Cuckoos that approached the playback and sang alternately raised and lowered their crests up to once per second, often rhythmically although not synchronized with their singing. Crest raising sometimes continued for several minutes. The birds’ bodies were usually hunched and their wings held slightly out and down with the dark alulas extended. Back feathers appeared ruffled in some subjects. Tails were usually fanned, although rarely widely. Individuals facing the playback speaker swayed from side-to-side without pivoting.

Vocal behavior with approach.—After closely approaching playback of *sem-fim*, all 13 subjects uttered bouts of *wee*-series songs (Table 1). None uttered any *sem-fim* until much later. We avoided pseudoreplication (see

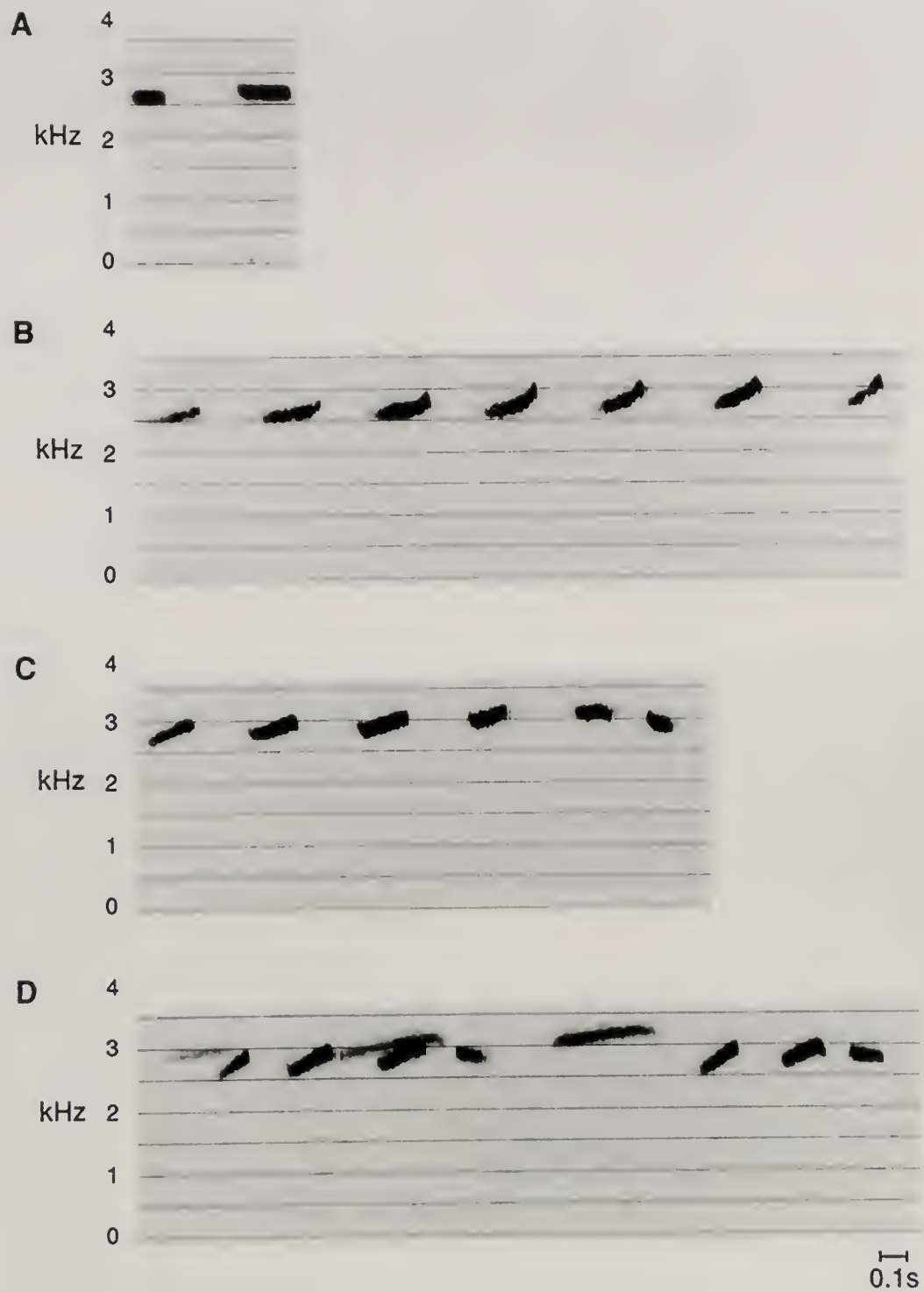


FIG 1. Examples of songs from four different individuals. (A) *sem-fim*, (B) simple *wee*-series song, (C) elaborated *wee*-series song, (D) a *feeee*-series song of three components, overlapping the first *wee*-series of a couplet of *wee*-series songs by a nearby individual.

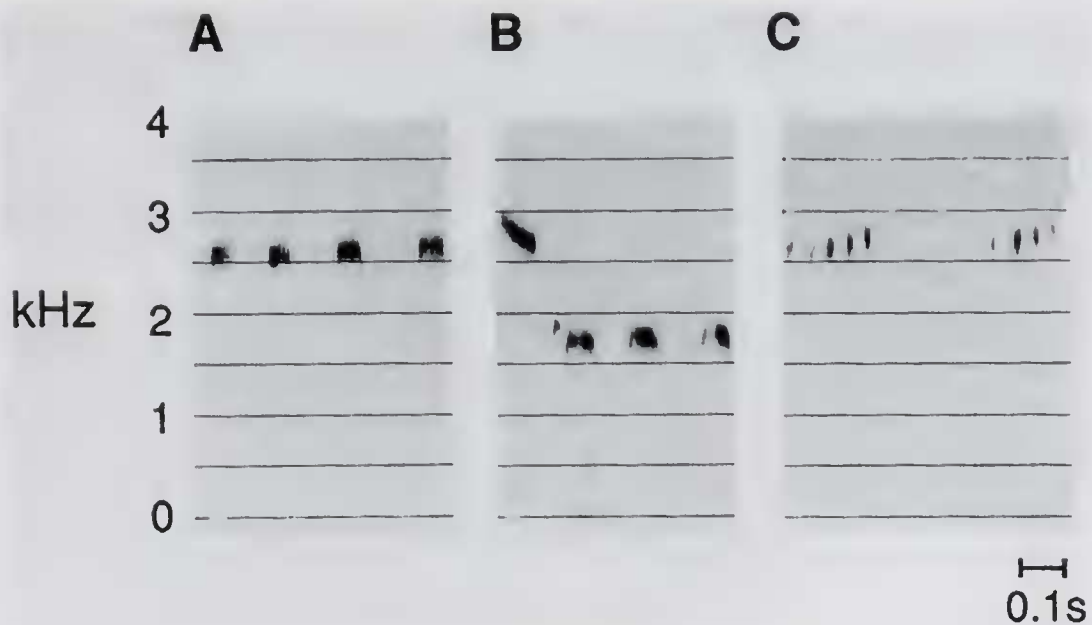


FIG 2. Examples of brief, variable tones (A) and (B) from one individual, (C) from another.

Kroodsma 1989) by using playback stimuli recorded from six different subjects (Sign test: $P = 0.03$).

One subject heard only *wee*-series playback. Like the others, it approached and sang *wee*-series songs. We also played *wee*-series to 1 of the initial 13 subjects after it had approached *sem-fim* playback and begun *wee*-series singing; it continued its *wee*-series. We returned 40 min later, long after it had reverted to *sem-fim* singing, and played that same *wee*-series stimulus. It again approached, singing long *wee*-series. Neither it nor the last bird sang elaborated *wee*-series.

After we stopped playback, nine subjects eventually changed to *sem-fim* bouts. Four others became silent. We ceased recording the remaining subject before it changed.

After approaching the playback speaker closely, a subject typically progressed from silence to brief, variable vocalizations, then to a bout of lengthening *wee*-series. When the speaker was moved and a subject made successive approaches, long *wee*-series songs came more quickly after each move, although the first song after an approach flight was rarely the longest. Four subjects shifted from long simple to long elaborated *wee*-series songs.

Brief tones occurred only in transitional phases. At least 11 subjects approached the speaker silently and eventually uttered such brief tones before bouts of *wee*-series songs.

At least four subjects uttered brief tones as they reverted to *sem-fim* singing.

Only two subjects vocalized during approach movements. Neither was close to the speaker. One uttered shortened vocalizations and condensed variants of short *wee*-series songs during two flights and two runs. The other uttered an 8 component *wee*-series song while running along a branch, then came no closer.

The only individual to utter *feeee* during trials was a bird close to our subject, perhaps its mate. It sang once and was overlapped by a *wee*-series song of the subject before the subject approached the speaker.

Bouts of *sem-fim* were heard from eight individuals in addition to our experimental subjects. Prevalence of *sem-fim* songs is consistent with the evidence from preplayback samples: 11 of 13 subjects that were vocal before playback were singing *sem-fim*. The two exceptions were singing *wee*-series in the pre-dawn chorus, when *wee*-series songs are common. *Sem-fim* was the most commonly uttered song type (Table 1) of birds that were not interacting closely.

Twice our playbacks resulted in neighbors approaching within 40 m of each other. They countersang *wee*-series songs and continued singing long after we ceased playback. We saw no close spontaneous encounters. Distant but audible neighbors all sang *sem-fim*.

Five individuals sang *wee*-series songs, primarily in crepuscular periods. Each apparently duetted with another individual that uttered *feeee*-series songs. The *wee*-series singer tended to produce many quick couplets of songs (see Fig. 1D). Couplets were otherwise recorded only from two subjects that did not approach the speaker. Members of each of the five dyads were closely attuned: 36 of the 37 recorded *feeee*-series songs were overlapped by a *wee*-series song. The dyad birds were much closer to each other than *sem-fim* singing neighbors ever were. We played the recorded song, but only one *wee*-series singing individual (mentioned above) approached the speaker. Its unseen companion went silent.

DISCUSSION

The three easily distinguished song types of Striped Cuckoos were associated with the following different activities: individuals that were not otherwise interacting and were not close to neighbors sang long bouts of *sem-fim*. All individuals that countersang against close neighbors or that had closely approached playback, sang *wee*-series songs. *Feeee*-series songs occurred only in apparent duets. All individuals singing *sem-fim* stopped after closely approaching the speaker. After a period of silence, most uttered faint, brief, marginally detectable vocalizations, then sang increasingly louder *wee*-series songs.

During its initial, faint singing each subject remained perched, often within cover, vocally probing to elicit responses from the simulated, unseen intruder. Faint singing may be a wary negotiating move that is audible only to nearby listeners. Negotiations are continuing exchanges of signals without committing to attack or another behavior as each participant assesses the other in a competitive situation (see Smith 1977b, 1985, 1997; Hinde 1985; Colmenares 1991). Faint vocalizations may not be loud enough to attract the attention of this species' hosts or predators. When near the site of a recent playback, the subjects' *wee*-series songs became louder and longer, then usually changed gradually into loud *sem-fim* singing.

Brief tones were uttered primarily during transitions from silence to *wee*-series when subjects were behaving warily, and less often when subjects reverted from *wee*-series to

sem-fim. Such subjects had not engaged in active confrontation. Their faint tones correlated with an investigative, probing phase of approach, similar to the *churr* song form of *Myiarchus crinitus* (Smith and Smith 1996a).

In the two close countersinging events, neighbors approached to within 50 m and sang *wee*-series songs. Because none attacked, *wee*-series do not appear to indicate a high probability of immediate escalation from approach to fighting. Furthermore, *wee*-series songs were uttered both in duets (by one participant) and in encounters by opponents. In several tyrannids (*Contopus virens*, Smith 1988; *Tyrannus tyrannus*, Smith and Smith 1992; *Myiarchus crinitus*, Smith and Smith 1996a), the song types used in interactions with neighbors were also used with intruders and mates. Thus, such songs provide information only about the probability of the singer initiating interaction, and not about some specific behavioral subset such as disputing with a neighbor or joining a mate.

The *feeee*-series song was not given in responses to playback. It was uttered by birds that were near *wee*-series singing individuals and may have been mates duetting. Sick (1953) described *feeee* in duets of mates. In our interactive playback studies of many species of tyrannids, furnariids, and tropical parulines, mates have vocalized in response both to playback stimuli and to each other (Smith 1996).

Our studies have now shown that the non-passerine Striped Cuckoo resembles diverse passerines in having different songs that correlate with different extents to which a singer actively promotes close interaction (i.e., either approaches or stays put, singing, leaving further initiative to other individuals). That singing can provide such information may thus be of fundamental importance when separated individuals must choose whether to interact more closely.

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